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Quantifying Responses to Hybrid Striped Bass Predation across Multiple Trophic Levels: Implications for Reservoir Biomanipulation

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Abstract.—Top-down effects from piscivores to phytoplankton have been documented in north temperate lakes, thus permitting managers to regulate these food webs. From our review of the literature, reservoir trophic interactions appear less amenable to biomanipulation owing to the presence of a fast-growing, omnivorous planktivore, gizzard shad *Dorosoma cepedianum*. If reservoir zooplankton can be enhanced by reducing gizzard shad through biomanipulation, this could increase survival of food-limited early life stages of sport fishes dependent on zooplankton and could improve water clarity by reducing phytoplankton. To quantify this potential, we evaluated responses of age-0 gizzard shad, crustacean zooplankton, and phytoplankton to the addition of hybrid striped bass *Morone saxatilis* × *M. chrysops* (22 kg/ha) to four of eight 0.4-ha ponds. Hybrid striped bass nearly eliminated age-0 gizzard shad from ponds within 10 d after being stocked, which permitted zooplankton density and size to increase but had no effect on phytoplankton. These pond results independently confirmed the relationships among zooplankton density, zooplankton production, and age-0 gizzard shad density that had been developed previously in 1-m³ enclosures. Only reservoirs with fewer than 10 age-0 gizzard shad/m³ and daily zooplankton production greater than 220 mg/m³ may be amenable to biomanipulation; these conditions occurred in our ponds due to hybrid striped bass piscivory and high zooplankton productivity. About 5% of Ohio reservoirs possess these two characteristics, which makes the potential for improving sport fish recruitment by reducing age-0 gizzard shad abundance a limited option for reservoir managers.

The trophic cascade hypothesis provides an intuitive understanding of top-down effects of fishes on lower trophic levels, given existing nutrient lev-

els (Carpenter et al. 1985, 1987; McQueen et al. 1989; Carpenter and Kitchell 1993). Top-down trophic interactions are common at the piscivore–planktivore, planktivore–zooplankton, and zooplankton–phytoplankton levels (DeMelo et al. 1992) in natural lakes because planktivores most

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TABLE 1.—Summary of published studies that quantified response of shad (*Dorosoma* spp.) populations to introduction of *Morone* spp. Studies were grouped by predator species and perceived success of shad control. Types of control relate to abundance (abnd) and size of shad populations; "no data" means response parameters were not discussed. GS = gizzard shad, TS = threadfin shad, and NA = not applicable.

Lake	Lake area (ha)	Prey species	<i>Morone</i> stocking density (fish/ha)	Pre- <i>Morone</i> data?	Statistical treatment of data?	Type of control	Study
Striped bass—successful control							
Keystone Reservoir, Oklahoma	10,643	GS	Mean = 51.7 fry across 5 years	No	No	Size	Combs (1979, 1982a, 1982b)
Smith Mountain Lake, Virginia	8,337	GS	Up to 97.1 fingerlings; mean = 36.5	No	NA	Abnd	Ney et al. (1988); Moore et al. (1987)
Lake Mead, Arizona-Nevada	6,000,000	TS	0.0098 fish	No	No	Abnd	Persons and Dreyer (1987)
Lake Powell, Arizona-Utah	64,000	TS	0.3–0.5 fingerlings	No	No	Abnd	Gustaveson et al. (1984, 1990)
Lake Mendocino, California	684	TS	5.0–7.5 fingerlings, adults	No	No	No data	Hanson (1980); McCammon and von Geldern (1979)
Millerton Lake, California	1,980	TS	6.25 fingerlings, yearlings, adults	No	No	No data	Hanson (1980); McCammon and von Geldern (1979)
Lake Hunter, Florida	40	GS, TS	37.5 fingerlings	Yes	No	Abnd	Ware (1974)
Lake Julianna-Mattie, Florida	800	GS, TS	25 fingerlings	Yes	No	Abnd	Ware (1974)
Herrington Lake, Kentucky	1,044	GS, TS	2–50 fingerlings	No	No	No data	Axon (1979)
Lake Texoma, Oklahoma-Texas	35,600	GS, TS	>1 million fry	No	No	GS—size; TS—abnd	Harper (1982); Harper and Nammanga (1986); Mauck (1986); Matthews et al. (1988)
Lake E. V. Spence, Texas	6,000	GS, TS	12.4–24.7 fingerlings	No	No	Abnd, size	Morris and Folis (1979)
Striped bass—unsuccessful							
Lake Wateree, South Carolina	5,548	GS, TS	72 fingerlings	Yes	No		Nash et al. (1988)
Striped bass—no conclusion							
Lake Nottely, Georgia	1,692	GS	0.1–24.8 fish	No	No	^a	England (1977)
D'Arbonne Lake, Louisiana	6,000	Shad	723,000 fingerlings across 13 years	No	No		Walker (1977, 1979)
Toledo Bend Reservoir, Louisiana	72,640	Shad	2,642,000 fingerlings across 13 years	No	No		Walker (1977, 1979)
Hybrid striped bass—successful							
Spring Lake, Illinois	101	GS	20–30 fingerlings	No	No	Abnd, size	Douglas (1986); Jahn et al. (1987)
Lake Bastrop, Texas	367	GS, TS	25 fish	No	No	GS—none; TS—abnd	Crandall (1979)
Hybrid striped bass—unsuccessful							
Hamms Lake, Oklahoma	40	GS	500–1,000 fry	Yes	No		Kleinholz and Maughan (1984)
Lake Carl Blackwell, Oklahoma	1,400	GS	214 fry	^b	^c		Kleinholz and Maughan (1984); Muoneke et al. (1987)
West Point Reservoir, Alabama-Georgia	10,121	GS, TS	84–150 fry, fingerlings	No	No		Ott and Malvestuto (1984)
Storm Creek Lake, Arizona	170	GS, TS	19.4–58.9 fingerlings	Yes	No		Ebert et al. (1988)
Lake Osborne, Arizona	144	GS, TS	21–338 fingerlings	Yes	No		Morello (1987)
Clarks Hill Reservoir, Georgia	28,340	GS, TS	18–41 fry, fingerlings	No	No		Germann (1985)

TABLE 1.—Continued.

Lake	Lake area (ha)	Prey species	Morone stocking density (fish/ha)	Pre-Morone data?	Statistical treatment of data?	Type of control	Study
Hybrid striped bass—no conclusion							
Cherokee Reservoir, Tennessee	12,591	GS	6.4 fingerlings	No	No		Bishop (1968); Saul and Wilson (1984)
Striped bass and hybrid striped bass—successful							
Wolf Creek Cooling Lake, Kansas	2,036	GS, TS	Unknown	No	No	Abnd	Haines (1991)
White bass—successful							
Elephant Butte Lake, New Mexico	16,327	GS	Unknown	No	No	Abnd, size	Jester and Jensen (1972)

^a Size of gizzard shad shifted, but this could not be attributed to the striped bass.

^b Pre-Morone data was included by Kleinholz and Maughan (1984), but not by Muoneke et al. (1987).

^c Statistics were used by Muoneke et al. (1987), but not by Kleinholz and Maughan (1984).

often consume zooplankton and because large zooplankton grazers (i.e., *Daphnia* spp.) are abundant. In a management sense, the trophic cascade hypothesis has been used to justify biomanipulation of communities to reduce abundant populations of planktivorous fishes (Stewart et al. 1981) or to improve water clarity in north temperate lakes (Carpenter et al. 1985; Shapiro and Wright 1984; Benndorf 1990; Kitchell 1992).

In reservoirs, resident piscivores frequently do not control the abundance of prey fishes. Gizzard shad *Dorosoma cepedianum* are especially hard to control because of their high fecundity (Vondracek and LeHew 1991), rapid growth, and limited vulnerability to piscivores (Adams and DeAngelis 1987; Johnson et al. 1988b; Hambright et al. 1991; Stein et al. 1995). Simultaneously, gizzard shad impose control on lower trophic levels by eliminating crustacean zooplankton populations (Drenner et al. 1982a, 1982b; Dettmers and Stein 1992; DeVries and Stein 1992). However, age-0 gizzard shad are not resource-limited by zooplankton because they can successfully consume phytoplankton and detritus (Miller 1960; Bodola 1966).

Omnivorous gizzard shad thrive in reservoirs (Summers and Axon 1980); they persist at high densities even after early summer zooplankton populations decline. By exploitatively competing for limited zooplankton in early summer, age-0 gizzard shad can reduce growth, survival, and abundance of other age-0 fishes (Guest et al. 1990; DeVries et al. 1991). Further, large reductions in zooplankton abundance do not result in increased phytoplankton in reservoir enclosures unless *Daphnia* spp. occur at densities greater than 40 individuals/L (Dettmers and Stein 1996). Thus,

trophic interactions in reservoirs containing gizzard shad seem weakly linked owing to (1) omnivory and fast growth by gizzard shad (making them invulnerable to resource depletion and piscivores) and (2) absence of large-bodied herbivorous zooplankton. Consequently, gizzard shad may regulate reservoir communities from the middle of the food web by affecting trophic levels above and below (Stein et al. 1995).

Even given this bleak outlook for biomanipulation, resource managers seek to improve sport-fishing opportunities in reservoirs by reducing gizzard shad (Crandall 1979; Ott and Malvestuto 1984; Jahn et al. 1987; DeVries and Stein 1990). Introducing large-gaped, fast-growing piscivores that strongly overlap with gizzard shad in the open water could reduce gizzard shad abundance sufficiently to release zooplankton from predation, and thereby could enhance recruitment of sport fishes and increase herbivory by zooplankton.

Piscivores that exert strong top-down impacts in natural lakes, for example, largemouth bass *Micropterus salmoides* (Carpenter et al. 1987; Hall and Ehlinger 1989), northern pike *Esox lucius* (McQueen et al. 1989), and walleyes *Stizostedion vitreum* (Johnson et al. 1992), cannot regulate gizzard shad populations in reservoirs, despite their preference for gizzard shad (Carline et al. 1984; Johnson et al. 1988a; Wahl and Stein 1991). In fact, we could find no evidence in the peer-reviewed literature of successful reduction of shad (including threadfin shad *D. petenense*) by black basses (*Micropterus* spp.), percids, or esocids. Because *Morone* predators are frequently stocked to consume shad (Pritchard et al. 1978), we reviewed the literature to determine how such introductions

influenced shad, zooplankton, and phytoplankton. We compiled 69 papers that dealt with 190 introductions of *Morone* spp. Shad populations were monitored in 26 introductions (Table 1), but in only 7 were pre-*Morone* data included and in just 1 was statistical treatment of the data included. Of these 26 introductions, 15 resulted in some form of shad control. Effects cited were reduced shad abundance (7), changed shad size (1), and changed abundance and size (4). In three other cases, control of shad was claimed, but specifics were not given.

Given the perceived relative success of introduced *Morone* spp. at controlling gizzard shad abundance and that no other piscivore had been introduced for that purpose (DeVries and Stein 1990), we chose to use hybrid *Morone* to experimentally evaluate top-down effects that could conceivably cascade to zooplankton and phytoplankton. Hybrid striped bass *Morone saxatilis* × *M. chrysops* were used because warm Ohio reservoirs would compromise summer survival of striped bass *M. saxatilis*.

Methods

Our experiment was conducted at the Hebron State Fish Hatchery near Buckeye Lake in Licking County, Ohio. Eight ponds (0.4 ha each, mean depth = 1 m) were filled with water from a canal connected to Buckeye Lake; water was filtered through a 245- μ m microstrainer to eliminate any larval fishes yet permit colonization by zooplankton and phytoplankton. As an added precaution, inflow water was strained through a 500- μ m mesh saran sock at each pond. Ponds were full after about 7 d; thereafter a constant, low inflow compensated for evaporation and leakage across dikes.

We added 40 adult gizzard shad (about 5 kg/ha) in spawning condition to each pond on May 7, 1993, so that we could expect abundant age-0 gizzard shad without confounding the experiment with extensive adult effects. Hybrid striped bass ($N = 59$ per pond; 184–400 mm TL) were added to four randomly chosen ponds on May 28 at an initial density of 22 kg/ha. On that same day, we added 45 kg/ha common carp *Cyprinus carpio* (>250 mm TL) to all ponds to increase turbidity and thus more closely mimic reservoir conditions. We sampled age-0 gizzard shad, crustacean zooplankton (hereafter zooplankton), and phytoplankton weekly during May 13–July 15 to assess their responses to our piscivore manipulation. Gizzard shad were sampled May 13–June 23 with an ichthyoplankton net (0.5-m diameter, 500- μ m mesh)

towed at about 1.0 m/s at the surface of each pond. Total larval production during May 13–June 23 was estimated by summing pondwide larval abundance estimates across sampling dates. After June 9, we collected gizzard shad via shoreline seining with a 10-m-long, 6.25-mm-mesh seine by sampling three 10-m transects per pond. Zooplankton and phytoplankton were collected with an integrated tube sampler (72 mm inside diameter) that sampled the entire water column (DeVries and Stein 1991). Zooplankton were filtered through a 54- μ m-mesh net and preserved in 4% sucrose-formalin (Haney and Hall 1973). Hybrid striped bass diets and diel food consumption were quantified on June 17 and June 30. Trap nets were checked every 3 h over 24 h in two ponds. We weighed and measured all hybrid striped bass caught. Stomach contents were recovered by pulsed gastric lavage and then frozen.

During July 19–21, we drained all ponds, collected remaining fish, and placed them in raceways where we quantified biomass and size distribution. All hybrid striped bass were individually weighed (nearest 1 g) and measured (nearest 1 mm). Stomach contents were recovered as described above to quantify piscivore size selection. We determined size distributions of gizzard shad, common carp, and bluegills *Lepomis macrochirus* by individually weighing and measuring subsamples from each pond (range: 965–2,500 g). All fish not subsampled in each pond were sorted by species and weighed. Bluegills were incidentally introduced into three ponds when we added common carp on May 28. Age-0 bluegills did not appear in ponds until July 7 and never contributed more than 2% of age-0 fish biomass.

Up to 20 individuals of each zooplankton taxon in a sample were measured (nearest 0.01 mm) on a digitizing tablet viewed through a microscope drawing tube (Stahl and Stein 1994). These measurements provided size distributions and allowed us to calculate biomass via taxon-specific, length-dry weight regressions (Dumont et al. 1975; Bottrell et al. 1976).

Phytoplankton were concentrated by filtering water through a 0.45- μ m filter, then placed on a cover slip and cleared with 2-hydroxypropyl methacrylate. Cover slips were dried for 12 h, mounted on a slide (three slides per sample), and counted through a compound microscope with Nomarski optics at 200 \times and 400 \times magnification. At least 15 fields were counted at each magnification to achieve a coefficient of variation (100-SD/mean) less than 10% (St. Amand 1990). Edible algae were

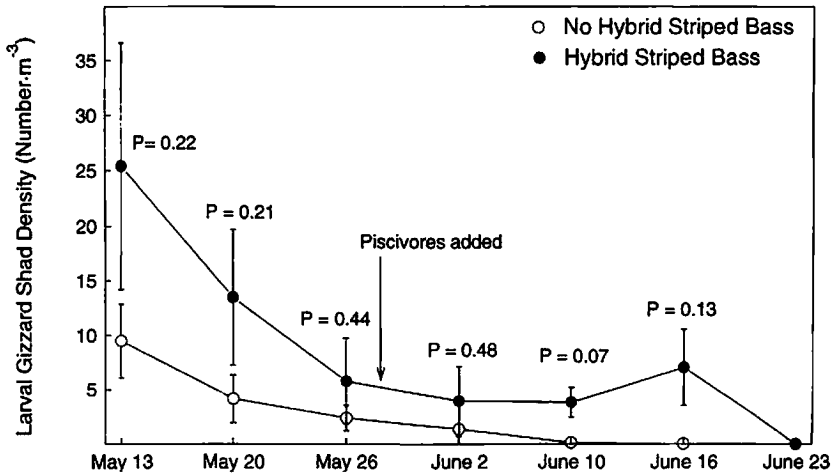


FIGURE 1.—Mean (\pm SE) density of larval gizzard shad (<25 mm TL) collected with a 0.5-m-diameter, 500- μ m-mesh ichthyoplankton net from eight 0.4-ha ponds at the Hebron State Fish Hatchery, Ohio, May 13–June 23, 1993. Hybrid striped bass were added to four ponds on May 28. The *P*-values represent results from *t*-tests on each date to determine if larval gizzard shad densities differed across treatments.

defined as diatoms, chrysophytes, and chlorophytes less than 35 μ m in the greatest axial linear dimension (GALD). Inedible algae included species of these taxa that were greater than 35 μ m GALD and all cyanophytes and dinoflagellates.

We calculated zooplankton production (dry weight) as the increase in mass of existing individuals plus the number of eggs produced each week (Culver and DeMott 1978). We used temperature-dependent growth and egg development equations to determine the time zooplankters spent in each stage (DeMott 1976; Bean 1980). Zooplankton growth plus fecundity provided taxon-specific production estimates. These estimates were then summed across taxa to generate estimates of total zooplankton production for each weekly interval.

We quantified diets of 214 age-0 gizzard shad collected by shoreline seining (up to five fish per pond per date). The pharyngeal pockets, esophagus, foregut, and gizzard were excised. We counted and measured all zooplankton consumed and calculated biomass consumed by using taxon-specific, length–dry weight regressions (see above).

Hybrid striped bass fish prey were measured (total, standard, or backbone length, depending on stage of digestion) and identified to species; partially digested prey were identified via structures resistant to digestion. We back-calculated prey weight at ingestion using length–weight relationships (Wahl and Stein 1991).

We analyzed treatment effects for age-0 gizzard

shad abundance, total zooplankton density, size, biomass, and production, and phytoplankton biovolume using split-plot repeated-measures analysis of variance, ANOVA (Maceina et al. 1994). Treatment effects were compared from the last sampling date prior to piscivore addition (May 26) until we ended the experiment (July 15). When necessary, data were normalized with a $\log_e(x + 1)$ transformation.

Results

Mean density of larval gizzard shad peaked at 25 fish/m³ in ponds to be stocked with hybrid striped bass and at 9 fish/m³ in ponds that were to remain piscivore-free on May 13 (Figure 1). Before hybrid striped bass were introduced, larval shad density did not differ between treatments on any given day (Figure 1) or across the entire larval sampling period (repeated-measures ANOVA; $F = 3.99$; $df = 1,3$; $P = 0.14$). Similarly, larval gizzard shad production in ponds with hybrid striped bass did not differ from that in piscivore-free ponds (*t*-test; $P = 0.18$), despite multiple spawning by gizzard shad that occurred only in the piscivore treatment. We inferred multiple gizzard shad spawning events in ponds containing hybrid striped bass because of the late larval peak on June 16 (Figure 1) and reduced size of larval gizzard shad relative to those from piscivore-free ponds at this time (Figure 2B).

Hybrid striped bass did not consume age-0 gizzard shad shorter than 25 mm. On June 17, when

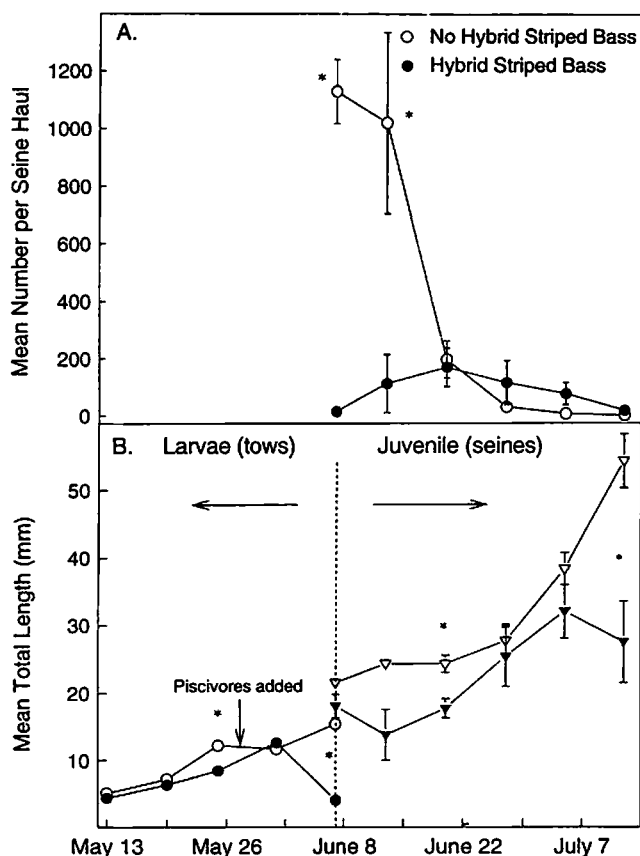


FIGURE 2.—Means (\pm SE); of (A) density of age-0 gizzard shad collected via shoreline seining June 9–July 15, 1993, and (B) total length of larval (<25 mm TL) and juvenile (≥ 25 mm) gizzard shad May 13–July 15 from eight 0.4-ha ponds. Hybrid striped bass were added to four ponds on May 28. In both panels, ponds containing hybrid striped bass are represented by solid symbols and predator-free ponds are represented by open symbols. Asterisks denote significant treatment effects ($P < 0.05$).

larval gizzard shad density was 8 fish/m³, seven hybrid striped bass had eaten 61 prey, only 1 of which was a fish. Similarly, on June 30, five hybrid striped bass had eaten 15 prey, but only 1 was a fish. We could not estimate the size for either of these fish prey due to advanced digestion. At draining, when 76% of hybrid striped bass diets ($N = 91$ guts) by weight consisted of fish, mean length (39.5 mm) of gizzard shad eaten ($N = 78$) was smaller than the mean length (57.4 mm) of age-0 gizzard shad ($N = 318$) in ponds (t -test; $df = 394$; $P < 0.0001$).

Hybrid striped bass reduced age-0 gizzard shad density relative to that in piscivore-free ponds, as measured by shoreline seining (Table 2; Figure 2A). This treatment effect resulted from the greater density of age-0 gizzard shad in piscivore-free ponds than in ponds with piscivores on June 9 and 16 (Figure 2A). The significant time \times treatment

interaction resulted from the steep decline of age-0 gizzard shad in piscivore-free ponds (Table 2; Figure 2A). Mean gizzard shad density declined to near zero in piscivore-free ponds after June 29 (Figure 2A), when the weight-specific amount of zooplankton in their guts declined to below that of gizzard shad in ponds with hybrid striped bass (t -test on each date; $df = 4$; $P < 0.04$). Further, mean gizzard shad length declined in ponds with piscivores relative to mean length in piscivore-free ponds (Table 2; Figure 2B), despite fewer gizzard shad in the piscivore ponds. A marginally significant time \times treatment interaction occurred because mean gizzard shad length in piscivore-free ponds increased during June 9–July 15, whereas mean gizzard shad length in ponds with hybrid striped bass only once exceeded 30 mm (Table 2; Figure 2B). However, at the end of the experiment there was no treatment effect on gizzard shad

TABLE 2.—Summary of split-plot repeated-measures ANOVA for various responses to our hybrid striped bass treatment in eight 0.4-ha ponds at the Hebron State Fish Hatchery, Ohio, during May 26–July 15, 1993. All response variables were measured only after hybrid striped bass were added (to four ponds) except for zooplankton density, which was measured both before and after the addition. Change refers to the direction of the response—increase (↑), decrease (↓), or no change (↔)—by each variable to the treatment and time main effects (the time × treatment interaction term cannot be classified by simple directional summary).

Response variable	Source of variation	df	Mean square	F	P	Change
Gizzard shad density	Treatment	1	1185770.11	33.67	0.01	↓
	Time	5	547197.91	12.67	0.0001	↓
	Time × treatment	5	595219.40	13.78	0.0001	
Gizzard shad length	Treatment	1	782.02	24.24	0.02	↓
	Time	5	519.43	18.35	0.0001	↑
	Time × treatment	5	68.72	2.43	0.06	
Log _e (pretreatment zooplankton density)	Treatment	1	0.02	0.00	0.95	↔
	Time	2	4.23	5.36	0.02	↑
	Time × treatment	2	0.88	1.12	0.36	
Log _e (posttreatment zooplankton density)	Treatment	1	21.74	24.98	0.02	↑
	Time	6	2.59	6.32	0.0001	↓
	Time × treatment	6	2.01	4.91	0.001	
Log _e (zooplankton size)	Treatment	1	1.13	11.36	0.04	↑
	Time	7	0.87	8.06	0.0001	↓
	Time × treatment	7	0.25	2.34	0.04	
Log _e (zooplankton production)	Treatment	1	40.60	8.44	0.06	↑
	Time	7	15.28	13.15	0.0001	↓
	Time × treatment	7	1.39	1.19	0.33	
Total phytoplankton biovolume	Treatment	1	5.69 × 10 ¹⁸	1.33	0.33	↔
	Time	6	2.68 × 10 ¹⁹	0.96	0.46	↔
	Time × treatment	6	2.68 × 10 ¹⁹	0.96	0.46	
Edible phytoplankton biovolume	Treatment	1	8.38 × 10 ¹¹	6.13	0.09	↔
	Time	6	2.07 × 10 ¹²	10.40	0.0001	↓
	Time × treatment	6	2.47 × 10 ¹¹	1.24	0.31	
Inedible phytoplankton biovolume	Treatment	1	1.14 × 10 ¹⁹	1.33	0.33	↔
	Time	6	8.92 × 10 ¹⁸	0.95	0.47	↔
	Time × treatment	6	8.93 × 10 ¹⁸	0.95	0.47	

length (*t*-test; *P* = 0.20), biomass (*t*-test; *P* = 0.40), or density (*t*-test; *P* = 0.43).

Mean zooplankton density was similar between treatments before hybrid striped bass were added, but afterwards it was greater in ponds with hybrid striped bass than in those without them (Table 2; Figure 3A). Zooplankton density was higher on several dates in ponds with piscivores than in those without them during June 10–July 6, but not later (Figure 3A). The time × treatment interaction resulted from zooplankton being nearly eliminated by gizzard shad but persisting at relatively constant, low density in piscivore-free ponds, whereas in the piscivore treatment, zooplankton remained abundant but not at a constant, high density (Table 2; Figure 3A). The overall response of zooplankton production was only marginally greater in ponds with hybrid striped bass than in those without them (Table 2; Figure 3C), despite greater zooplankton production in hybrid striped bass ponds on each date during June 10–July 6 (Figure 3C). Mean zooplankton size was larger in ponds with hybrid striped bass (Table 2; Figure 3B), primarily because average size declined in the piscivore-free

treatment during mid-June. The decline in mean zooplankton size in piscivore-free ponds after June 15 resulted in a significant time × treatment interaction (Table 2; Figure 3B). Top-down effects of hybrid striped bass did sustain a larger zooplankton size, but only beginning 4 weeks after piscivore addition, despite a faster response in zooplankton density.

Biovolumes of total, edible, and inedible phytoplankton did not respond to piscivore addition (Table 2; Figure 3D). No time × treatment effects were significant in any of our phytoplankton analyses, though edible phytoplankton declined through time, thus resulting in a significant time effect.

Mean zooplankton density in ponds during June 2–July 15 was negatively related to peak age-0 gizzard shad density, as estimated by shoreline seining, and positively related to mean zooplankton production (Figure 4). Age-0 gizzard shad density and zooplankton production explained 97% of the observed variation in mean zooplankton density across all ponds (Table 3). Further, this experiment illustrated the impact piscivores made in driving age-0 gizzard shad abundance to suffi-

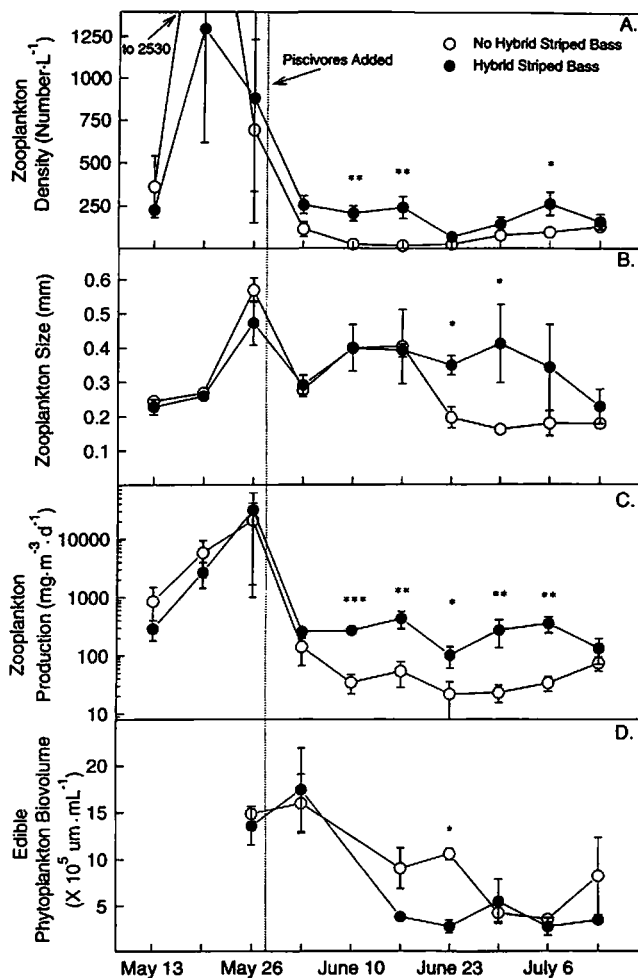


FIGURE 3.—Means (\pm SE) of (A) zooplankton density, (B) zooplankton size, (C) zooplankton production (dry weight), and (D) edible phytoplankton biovolume in eight 0.4-ha ponds at the Hebron State Fish Hatchery, Ohio, May 13–July 15, 1993. Hybrid striped bass were added to four ponds on May 28. Note that y-axis scales on all panels are arithmetic except for panel C, which is logarithmic. Asterisks denote significant treatment effects: $P < 0.05^*$; $P < 0.01^{**}$; and $P < 0.001^{***}$.

ciently low levels to permit zooplankton persistence. Incorporating phytoplankton main effect and interaction terms into the model (described in Table 3) provided no additional explanatory power to the observed pattern of zooplankton abundance.

We compared this model with a relationship developed by Dettmers and Stein (1996) from 1-m³ in-reservoir enclosures. Dettmers and Stein (1996) predicted that zooplankton persist at more than 100/L only if age-0 gizzard shad density is less than 10 fish/m³ and daily zooplankton production (dry weight) exceeds 220 mg/m³. Our pond relationship mimicked that from enclosures (test for

differences between regression lines; $F = 0.17$; $df = 3,40$; $P = 0.92$), thereby providing strong, independent confirmation of the processes by which age-0 gizzard shad density and zooplankton productivity determine zooplankton density (Figure 5). Hybrid striped bass reduced gizzard shad, consequently permitting mean zooplankton density to increase in piscivore ponds relative to that in piscivore-free ponds. We conclude that zooplankton persist only if age-0 gizzard shad density remains below 10 fish/m³ and daily zooplankton dry weight production exceeds 220 mg/m³ in the presence of hybrid striped bass.

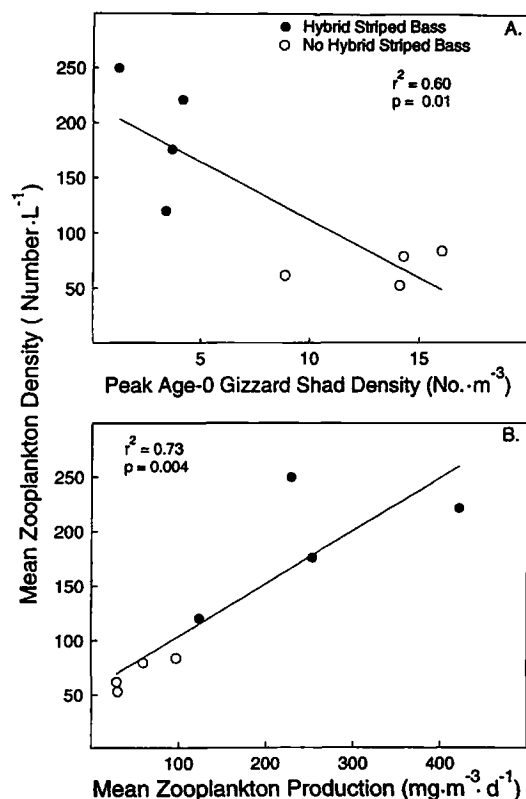


FIGURE 4.—Plots of mean zooplankton density June 2–July 15, 1993, as a function of (A) peak age-0 gizzard shad density, as measured by shoreline seining and (B) mean zooplankton production (dry weight) in eight 0.4-ha ponds at the Hebron State Fish Hatchery, Ohio. Each data point represents one pond.

Discussion

Few resident piscivore species are likely to reduce gizzard shad abundance in reservoirs, due to the predators' diet diversity and gape limitation (Saiki and Ziebell 1976; Hambright et al. 1991). Our review of the literature revealed that authors

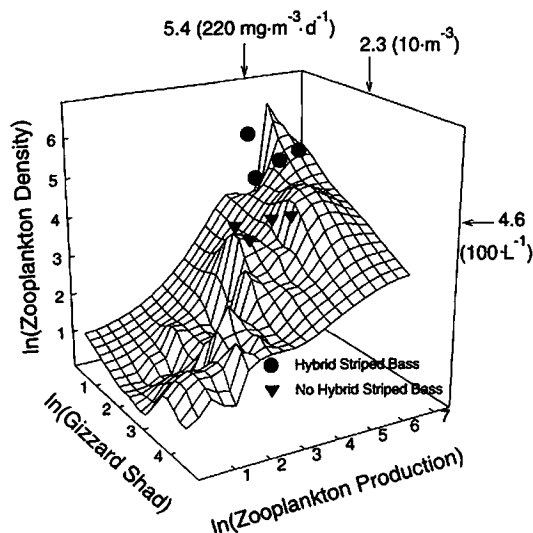


FIGURE 5.—Response surface (from Dettmers and Stein 1996; $\ln = \log_e$) of density of zooplankton remaining in 1-m³ enclosures after 28-d experiments, as functions of the density of age-0 gizzard shad in each enclosure and final zooplankton production (dry weight). Results from the present study are plotted with the response surface; each symbol represents one pond.

perceived that *Morone* predators commonly reduced shad abundance. However, almost all authors failed to apply appropriate statistical evaluation or to use adequate experimental design to validate this perception (sensu DeVries and Stein 1990). Thus, the literature data suggest, but are insufficient to allow us to conclude, that *Morone* spp. can control shad populations.

The literature review also suggested that system productivity was an important influence on the ability of *Morone* spp. to control shad. For example, declining threadfin shad abundance in Lake Mead, Arizona–Nevada was attributed to a combination of striped bass predation and declining phytoplankton abundance (due to reduced nutrient

TABLE 3.—Regression equations predicting zooplankton density in eight 0.4-ha ponds, with and without hybrid striped bass, and the regression summarizing all experiments in enclosures from Dettmers and Stein (1996) and ponds in the current study. The regression model was of the form $\log_e(\text{zooplankton density}) = a + b \cdot \log_e(\text{gizzard shad density}) + c \cdot \log_e(\text{zooplankton production})$. Coefficients d and e are indicator variables for hybrid striped bass presence and experiment type, respectively.

Experiment	Regression coefficient					F	P	R ²
	a	b	c	d	e			
Ponds, N = 8	3.43	-0.30	0.41			11.69	<0.0001	0.97
Ponds, N = 8	3.60	-0.54	0.53	0.54		250.10	<0.0001	0.99
Enclosures and ponds, N = 44	-0.75	0.12	0.86		1.11	111.62	<0.0001	0.89

availability after completion of an upstream dam; Persons and Dreyer 1987). In Lake Powell Utah-Arizona, increased striped bass abundance led to dramatic reductions in shad abundance, which was previously thought to be limited by resource availability in this oligotrophic system (Gustaveson et al. 1984, 1990). The only factor believed to have allowed threadfin shad to persist despite increased predation was the presence of turbid refuges in canyons and bays (Gustaveson et al. 1984).

Our pond experiment demonstrated that hybrid striped bass reduced age-0 gizzard shad, thus permitting zooplankton density to persist at greater than 100/L during June 2–July 15. However, increased zooplankton abundance, size, and production were not sufficient to reduce edible phytoplankton biovolume. Thus, hybrid striped bass can reduce age-0 gizzard shad and permit zooplankton to persist, at least in systems with high zooplankton productivity.

When piscivores were present, size of age-0 gizzard shad initially increased slowly relative to shad size in piscivore-free ponds because hybrid striped bass probably eliminated the largest individuals as they grew to a size that was vulnerable to predation early in the experiment. In ponds with hybrid striped bass, age-0 gizzard shad size averaged more than 25 mm only after July 7, whereas age-0 gizzard shad in piscivore-free ponds averaged nearly 25 mm by June 8. Despite the small relative size of age-0 gizzard shad in the piscivore treatment, the dry- to wet-weight ratio (one measure of their condition) was greater there than it was in ponds without hybrid striped bass during June 9–June 29, which reflected greater food availability for shad with piscivores present. But after June 29, age-0 gizzard shad grew well in piscivore-free ponds despite low zooplankton abundance, which was less limiting then, due to reduced gizzard shad abundance, than it was before June 29. Despite the likelihood that hybrid striped bass selected large age-0 gizzard shad early in the experiment, they selected small age-0 gizzard shad at the end of the experiment.

When age-0 gizzard shad are abundant and grow longer than 25 mm, their consumptive demand rapidly increases (Dettmers and Stein 1992), resulting in reduced zooplankton. Age-0 gizzard shad in our experiment depleted zooplankton in piscivore-free ponds probably because the shad grew beyond 25 mm by early June. Whereas weight-specific zooplankton consumption by individual age-0 gizzard shad was greater in our piscivore ponds after June 29, population consumption was lower then, owing

to lower densities and smaller size of shad in the presence of hybrid striped bass (as compared to piscivore-free ponds).

Reducing consumption by the age-0 gizzard shad population is necessary but not sufficient to permit abundant zooplankton to persist. In 1-m³ enclosures, zooplankton could be eliminated if production was low, even when age-0 gizzard shad density was less than 10 fish/m³ (Dettmers and Stein 1996). Zooplankton persisted in enclosures only when two conditions were fulfilled: (1) age-0 gizzard shad density was less than 10/m³ and (2) daily zooplankton dry weight production exceeded 220 mg/m³. In our pond experiment, mean daily zooplankton production after June 1 was 257 mg/m³ in ponds with hybrid striped bass, but was only 54 mg/m³ in piscivore-free ponds. These results explain why zooplankton persisted only in our piscivore treatment and provide support for the perception generated by our literature review that system productivity influences the potential for gizzard shad control.

Despite strong top-down zooplankton responses, edible phytoplankton biovolume was unaffected. This is consistent with results from north temperate lakes without abundant large zooplankton (Carpenter et al. 1985) and with the 1-m³ enclosure results, in which zooplankton could only influence phytoplankton when *Daphnia* spp. density exceeded 40/L (Dettmers and Stein 1996). In our piscivore ponds, *Daphnia* spp. density never exceeded 39/L after June 1. In addition, resuspension of nutrients by common carp may have permitted increased algal biomass, thus masking potential phytoplankton reductions by zooplankton (Havens 1993).

Zooplankton abundance can be sustained given high zooplankton productivity coupled with low age-0 gizzard shad abundance resulting from hybrid striped bass predation. The potential for piscivores to increase zooplankton abundance depends both on zooplankton productivity and age-0 gizzard shad density (Dettmers and Stein 1996). In turn, the success of piscivore manipulations, relative to improved sport fish recruitment, probably will depend on the density of zooplankton permitted to persist.

At least 100 zooplankters/L are required for reasonable recruitment of larval fishes (Werner and Blaxter 1980; Eldridge et al. 1981; Li and Mathias 1982). Thus, recruitment of bluegills and crappies *Pomoxis* spp. may improve if piscivores sufficiently reduce age-0 gizzard shad abundance, especially when other planktivores are rare. Such improved

recruitment may not be realized if hybrid striped bass consume these sport fish prey. However, hybrid striped bass survived poorly in small (<50 ha) Oklahoma reservoirs containing only bluegills (Layzer and Clady 1984). In a Texas reservoir containing 2–20 times more bluegill biomass than shad biomass, hybrid striped bass diets still consisted of 50–90% shad and only 10–20% bluegills by volume (Crandall 1979). Thus, hybrid striped bass are likely to exert only minimal predation on spiny-rayed sport fishes.

Piscivores may influence the potential for zooplankton persistence in individual reservoirs by consuming age-0 gizzard shad (see response surface, Figure 5). Hybrid striped bass shifted age-0 gizzard shad density to the left on our response surface, thus elevating zooplankton density. Effective predators of age-0 gizzard shad may permit a greater peak density of the shad to coexist with abundant zooplankton by quickly reducing age-0 gizzard shad as they grow beyond 25 mm, at which length the shad begin to intensively consume zooplankton. For instance, in our experiment, ponds without hybrid striped bass exhibited a mean peak density of age-0 gizzard shad (>25 mm) at 11.3 fish/m³, which is above the minimum threshold for biomanipulation, whereas the mean peak of age-0 gizzard shad density in ponds with piscivores was only 1.7 fish/m³.

Without considering these food web interactions, managers are unlikely to predict those reservoirs suitable for top-down responses. For instance, in 44% (21 of 48) of Ohio reservoir-years, age-0 gizzard shad density was below 10/m³ (Bremigan et al. 1991; DeVries et al. 1991; DeVries and Stein 1992; N. S. Donovan, Aquatic Ecology Laboratory, unpublished data). Of 21 reservoir-years, in only 3 (14%) was our daily zooplankton production threshold of 220 mg/m³ exceeded (Dettmers and Stein 1996; J. M. Dettmers and M. T. Bremigan, Aquatic Ecology Laboratory, unpublished data). Criteria for both age-0 gizzard shad density and zooplankton production must be met within a single reservoir for successful biomanipulation to occur. Assuming these criteria to be independent, we multiplied their probabilities to predict that about 5% of Ohio reservoirs have an age-0 gizzard shad density lower than 10 fish/m³ coupled with daily zooplankton production greater than 220 mg/m³, which would permit zooplankton densities higher than 100/L.

Top-down effects of hybrid striped bass reduced age-0 gizzard shad and increased zooplankton densities but did not cascade to phytoplankton. Im-

proved reservoir water clarity is unlikely through piscivore-induced responses, given the small size of zooplankton in most Ohio reservoirs (Bremigan et al. 1991; Aquatic Ecology Laboratory, unpublished data). However, biomanipulation may occur in reservoirs when zooplankton densities are higher than 100/L if piscivores maintain age-0 gizzard shad density at less than 10 fish/m³ and daily zooplankton production exceeds 220 mg/m³. Only about 5% of Ohio reservoirs are suitable for biomanipulation in this context; hence, the potential for improving sport-fish recruitment by increasing the zooplankton abundance through reducing age-0 gizzard shad is limited for reservoir managers.

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